Research

Plant invasions along mountain roads: the altitudinal amplitude of alien Asteraceae forbs in their native and introduced ranges

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Studying plant invasions along environmental gradients is a promising approach to dissect the relative importance of multiple interacting factors that affect the spread of a species in a new range. Along altitudinal gradients, factors such as propagule pressure, climatic conditions and biotic interactions change simultaneously across rather small geographic scales. Here we investigate the distribution of eight Asteraceae forbs along mountain roads in both their native and introduced ranges in the Valais (southern Swiss Alps) and the Wallowa Mountains (northeastern Oregon, USA). We hypothesised that a lack of adaptation and more limiting propagule pressure at higher altitudes in the new range restricts the altitudinal distribution of aliens relative to the native range. However, all but one of the species reached the same or even a higher altitude in the new range. Thus neither the need to adapt to changing climatic conditions nor lower propagule pressure at higher altitudes appears to have prevented the altitudinal spread of introduced populations. We found clear differences between regions in the relative occurrence of alien species in ruderal sites compared to roadsides, and in the degree of invasion away from the roadside, presumably reflecting differences in disturbance patterns between regions. Whilst the upper altitudinal limits of these plant invasions are apparently climatically constrained, factors such as anthropogenic disturbance and competition with native vegetation appear to have greater influence than changing climatic conditions on the distribution of these alien species along altitudinal gradients.

The spread of a species in a new range is limited by propagule pressure, abiotic factors and biotic interactions with competitors, consumers and mutualists, and all these factors may vary along environmental gradients such as of latitude, continentality and altitude (Hallet 2006, Dietz and Edwards 2006). Along altitudinal gradients, many factors change simultaneously across rather small geographical scales (Arévalo et al. 2005, Becker et al. 2005). Of particular importance for temperate plant species, mean temperatures and the length of the growing season decrease with altitude, whilst UV-B intensity increases (Körner 2007). Furthermore, the intensity and impact of anthropogenic activities, which are often associated with high propagule pressure, are often much reduced at higher altitudes (Parks et al. 2005).

Because populations close to the altitudinal limit of an alien species represent an invasion front, understanding what determines this limit can reveal which factors have the strongest influence on the progress of an invasion. Becker et al. (2005) found that the maximum altitude reached by alien plant species in the Swiss Alps tended to increase with time since introduction, and proposed that this relationship might reflect ongoing adaptation of invading populations.

However, human land use is also concentrated at low elevations (Nogués-Bravo et al. 2008), and so opportunities for the introduction and establishment of propagules generally decrease with altitude. Therefore, this relationship might also be explained by low propagule pressure (i.e. dispersal limitation) at high altitude, which has emerged as a major determinant of invasion success at both local (Von Holle and Simberloff 2005) and regional (Rouget and Richardson 2003) spatial scales (Colautti et al. 2006).

One way to investigate the relative importance of climatic factors compared to other factors such as propagule pressure and biotic interactions is to study the distribution of alien plants along mountain roads. Along a roadside in mountainous regions, climatic conditions change sharply from low to high altitude, whilst habitat factors (e.g. vegetation characteristics, disturbance) often remain relatively constant. Mountain roadsides are also punctuated along their length by ruderal sites more disturbed than the normal verge (e.g. near settlements, commercial centres, parking areas etc.), and these may be important both as sources of propagules and for facilitating establishment (Marcus et al. 1998, Johnston and Pickering 2001, Godfree

et al. 2004). Thus, roads serve not only as conduits for the dispersal of alien species (Tyser and Worley 1992, Parendes and Jones 2000, Johnston and Johnston 2004, Christen and Matlack 2006) but provide a habitat that is typically disturbed and nutrient-rich, both of which promote the establishment of alien (and native) species (Burke and Grime 1996, Davis et al. 2000).

To understand the processes influencing plant invasions along environmental gradients in mountains, it is important to compare the distributions of alien species in both the native and introduced ranges. Such comparisons can help determine how distributions, and the factors which underlie them, are altered in the new range, and so clarify the processes responsible for the spread of alien species (Bossdorf et al. 2005, Hierro et al. 2005). Furthermore, a reciprocal approach using species both native and introduced to each area studied can reveal the relative importance of region-specific effects on invasion patterns.

Here we report on a reciprocal study of the distribution of eight species of Asteraceae forbs in roadside verges and ruderal sites along altitudinal gradients. We hypothesised that due to low propagule pressure and a lack of adaptive/plastic responses to high altitude conditions, plants show a more restricted altitudinal distribution in the introduced range. Because of this, the establishment of alien plants, particularly at high altitude, will be restricted to ruderal sites that provide not only more propagules but also offer refuge from competition with natives (Petryna et al. 2002). For the same reason, we expected alien establishment to decline with decreasing disturbance away from the roadside.

Materials and methods

Species

We selected eight ruderal forb species in the Asteraceae – four native to Europe but invasive in North America (*Cirsium arvense*, *Cirsium vulgare*, *Cichorium intybus* and *Lactuca serriola*), and four native to North America but invasive in Europe (*Conyza canadensis*, *Erigeron annuus*, *Matricaria discoidea* and *Solidago canadensis*) – representing a range of breeding systems and life-histories (Table 1). The *Solidago canadensis* complex is taxonomically difficult: according to the most recent revision (Semple and Cook 2006), the taxon occurring in the Wallowa Mountains is *S. lepida* whereas that found in Europe is *S. canadensis*, a native of eastern North America. Nonetheless, although the two taxa are now recognised as separate species, they are closely related within the same species complex.

Study regions

The study was conducted in canton Valais in southern Switzerland (46°10′N, 7°20′E), and in the Wallowa Mountains in northeast Oregon, USA (45°15′N, 117°20′W), two mountain areas with temperate, continental climates (Fig. 1). Topography is steeper in the Valais than the Wallowas, and several peaks extend above 4000 m a.s.l., whilst only few peaks in the Wallowas reach above 2500 m a.s.l. (Fig. 1). The regions are similar in terms of mean annual temperature and heat sum (degree days $\geq 5°C$) over the growing season (April–September), which also decrease at a similar rate with altitude in both regions (Fig. 2). However, annual precipitation is higher in the Valais (Fig. 2) and is distributed more evenly over the year than in the Wallowas, where most rain and snow falls in winter and spring. The annual temperature range is greater in the Wallowas (36.4°C) than in the Valais (24.8°C) over the same altitudinal range (1000–2000 m a.s.l.), and the Wallowas have on average 5.3 frost days more during the growing season (Fig. 2). However, the climate of the Valais has become slightly warmer and drier in recent years (Rebetez and Dobbertin 2004).

The Valais is more densely populated than the Wallowas, especially the central Rhône valley bottom and sides up to 900 m a.s.l. which are dominated by settlements, agriculture and viniculture. The continental mountain belt (ca 900–1900 m a.s.l.; Landolt and Urbanska 2003) consists of a patchwork of agriculture/pasture (21%), forest (60%; dominated by *Pinus sylvestris*) and urban areas (6.5%; Glenz et al. 2001). *Pinus sylvestris* is replaced by *Picea abies*, *Pinus cembra* and *Larix decidua* at higher altitudes (ca 1900–2400 m a.s.l.), with shrub communities giving way to the alpine zone above ca 2400 m a.s.l. (Landolt and Urbanska 2003). The alpine zone is impacted by tourism, sheep grazing and the ski-infrastructure in some areas.

Parts of the Wallowas are used for cattle ranching and timber extraction, but most of the area has been designated as National Wilderness. The montane zone (ca 1000–1900 m a.s.l.) of the Wallowas is dominated by *Pinus ponderosa* and *Pseudotsuga menziesii* forest and the subalpine forest (ca 1900–2400 m a.s.l.) by *Larix occidentalis* and *Abies lasiocarpa*, with the true alpine zone beginning at around 2500 m a.s.l. (Pohs 2000, Parks et al. 2005). Lower altitudes (<ca 1000 m a.s.l.) are dominated by bunchgrass

Table 1. Geographic and life-history characteristics of the study species.

Species	Origin	Perenniality	Breeding system	Introduction to study region
Cirsium arvense (L.) Scop.	Eurasia	Perennial	Out., veg.	ca 1900*
Cirsium vulgare (Savi) Ten.	Eurasia	Biennial	Mixed	ca 1900*
Cichorium intybus L.	Europe	Perennial	Out.	ca 1900*
Lactuca serriola L.	Eurasia	Annual	Mixed	ca 1900*
Conyza canadensis (L.) Cronq.	N America	Annual	Mixed	Since 1800†
Erigeron annuus (L.) Pers.	N America	Annual	Apomictic	Since 1928‡
Matricaria discoidea DC.	N America	Annual	Selfing	1914†
Solidago canadensis L.	N America	Perennial	Out., veg.	1948†

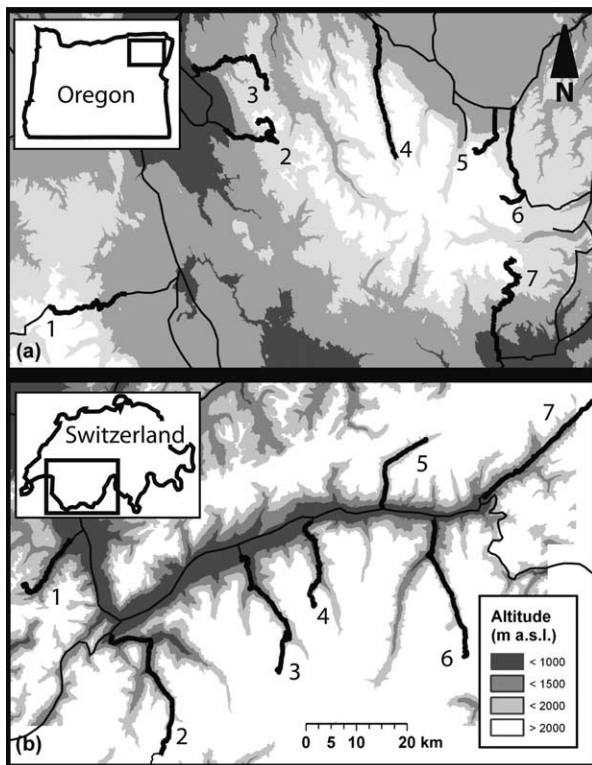*See text; †Hegi (1979); ‡ Hess et al. (1972). "Out.", outcrossing; "veg.", vegetative.

Figure 1. Altitude contour maps of the two study areas with the major-road systems (surveyed sections shown in bold). In ((a) Wallowa Mountains), the roads are (1) the Elkhorn Scenic Byway, (2) Moss Springs road, (3) Mount Harris Loop, (4) Lostine River road, (5) Mount Howard road, (6) Wallowa Mountain Loop and (7) Fish Lake road. In ((b) Valais), the roads link the Rhone valley to (1) Planachaux, (2) the Grand-St.-Bernard pass, (3) Arolla, (4) the Moiry dam, (5) Fafleralp, (6) the Mattmark dam and (7) the Furka pass. Note that the full extent of road (7) is not shown.

(*Pseudoroegneria spicata* and *Festuca idahoensis*) and sagebrush (*Artemisia* spp.) steppe with agriculture and cattle ranching in the valleys surrounding the central massif (Parks et al. 2005).

In each region, we chose seven frequently used roads that extended across a wide altitudinal range. In the Valais, two of the roads sampled link the main valley to major passes (Furka and Grand-St.-Bernard passes), two end at dams (Stausee Mattmark and Barage de Moiry) and the remaining three end at alpine villages (Arolla, Planachaux and Fafleralp; Fig. 1b). All these roads are heavily used and have settlements and centres of commerce along their lengths. The roadside vegetation comprises native and alien ruderal species. The latter have presumably been introduced accidentally by traffic and industrial activities or have escaped from gardens. Roadside verges are mown at regular intervals during the summer.

The road system in the Wallowas was constructed primarily to service mining activities in the mountains around the turn of the 20th century (Pohs 2000), and now provides access for grazing allotments, timber harvest and recreation. Except for the upper part of the Mount Howard road, all the roads sampled are open to motor vehicles (Fig. 1a), and the road system is generally more highly connected than in the Valais. Two roads end at fire towers

(Mount Harris Loop and Fish Lake Road), three at trail heads (Lostine River, Elkhorn Scenic Byway and Wallowa Mountain Loop) and two at mountain summits (Moss Springs Road and Mount Howard). Most roads in the mountains are gravel, and receive little maintenance apart from being graded annually. Only the Elkhorn Scenic Byway and Wallowa Mountain Loop are paved along most of their length. The former is the only sampled road to be located outside of the Wallowas, across the valley in the neighbouring Elkhorn Range (Fig. 1a). The roadside vegetation comprises a mixture of native and alien shrubs, grasses and forbs. Some of the alien species were probably introduced accidentally and have established since the road network was constructed, while others were present in seed mixtures used to stabilise slopes during road construction or as forage species for livestock (Dyrness 1975).

Data collection

The study was conducted between July and August 2005 in the Valais, and August and September 2006 in the Wallowas. The climate during this period in the Valais (Sion: 20.1°C/34 mm precipitation) was warmer and drier than average (18.5°/52 mm), but in the Wallowas (La Grande: 17.6°C/24 mm) was slightly cooler and wetter than average (18.2°/21 mm) (means of two low altitude weather stations; <http://www.meteoschweiz.ch>, <http://www.wrcc.dri.edu>). We sampled each road from bottom to top using plots placed at 25 m altitudinal increments. The top of the road was defined as its highest point and the bottom as its junction with the main road network surrounding the mountains, where there were no appreciable changes in altitude over small spatial scales. We used plots of 150×2 m to capture the relatively scarce occurrences of the species in the roadside vegetation. These were placed along the verge on the right hand side of the road travelling upwards, with the outside edge of the longest side running parallel to the first occurrence of the vegetation on the verge. Within each plot, we recorded the presence/absence of the target species, the approximate tree cover (<33, $33-67$, >67%) and the dominant vegetation type within 10 m of the road. At the end of each transect the altitude and a waypoint were recorded using a Garmin eTrex Legend® handheld GPS device. In total 378 verge plots were sampled in the Valais, and 296 in the Wallowas.

We also sampled a number of ruderal sites (Valais, 265 sites; Wallowas, 139 sites) located along the right hand side of each road. These sites, which included parking areas, road-servicing areas, small industrial areas/yards, waste areas, trail heads and campsites, were generally more disturbed than the roadside verges. They were sampled by searching an area of up to 300 m^2, though many sites were smaller than this (Valais, 165; Wallowas, 106). On average, small sites in the Valais were located 127 m higher than full-sized sites (Student's t $=2.24$, DF $=258$, p <0.05). In the Wallowas there was no significant difference between the mean altitudes of the two types of site (Student's t $= -1.69$, DF $=135$, p >0.09).

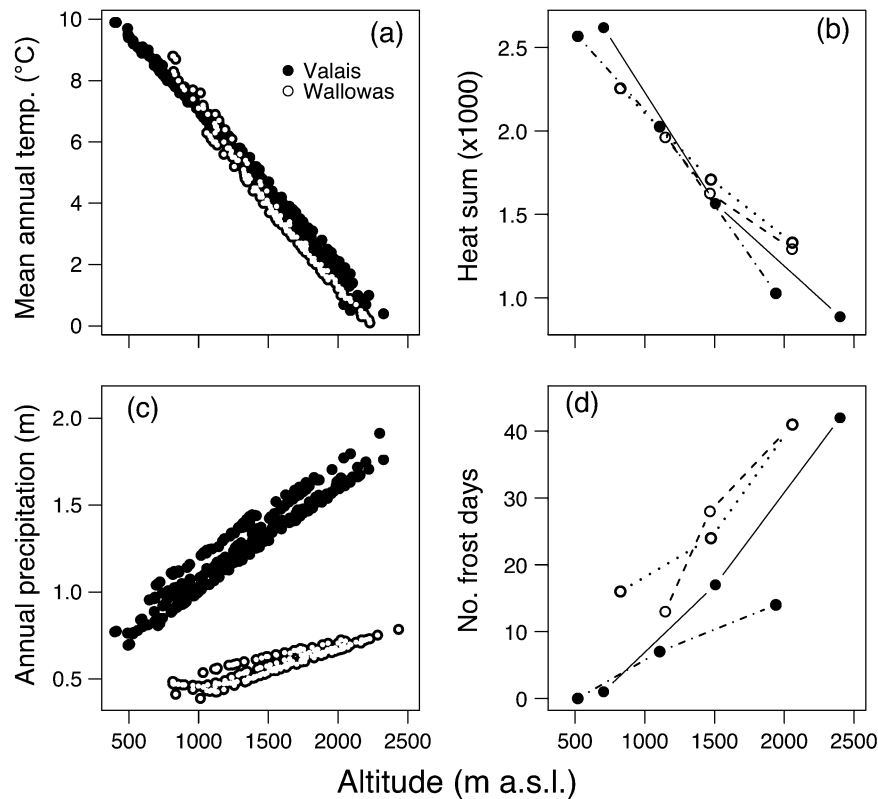In a separate survey conducted in 2006 (June in the Valais, August/September in the Wallowas), we compared

Figure 2. Variation in (a) mean annual temperature, (b) annual precipitation, (c) heat sum (degree days >5°C) and (d) the number of frost days (min. temperature <0°C) with altitude in the study regions. In (a) and (b), data were obtained from WORLDCLIM climatic interpolations for each surveyed location (Hijmans et al. 2005). Data in (c) and (d) were collected between April and September 2005 along two roads in the Valais (Visp to Furka pass, solid line; Martigny to Grand St. Bernard pass, dot-dashed line) and the Wallowa Mountains (Mount Harris Loop, dotted line; Moss Springs road, dashed line; Alexander et al. in press). Panels (b) and (d) are reproduced from Ecology with kind permission of the ESA.

species occurrences at and away from the roadside along six roads (Valais: roads to Grand-St.-Bernard, Arolla, Stausee Mattmark; Wallowas: Mount Harris Loop, Moss Springs road, Fish Lake road). Along each road, 11 transects (33 in each region) were placed at regular altitudinal increments between ca 500–2100 m a.s.l. in the Valais, and ca 900–2300 m a.s.l. in the Wallowas. Each transect consisted of one 2 × 12.5 m plot set out along the roadside with the longest edge parallel to the verge, and four to seven 5 × 5 m plots away from the roadside. A different plot shape was used at the roadside to ensure that only verge vegetation (which was often only ca 2 m wide) was sampled. To capture the transition from the verge to the adjoining vegetation, plots were placed at intervals of 10, 50 and 100 m from the roadside. Thereafter plots were placed at 100 m intervals up to 500 m, where the terrain permitted. In total 206 plots were sampled in the Valais (33 roadside, 173 non-roadside) and 224 in the Wallowas (33 roadside, 191 non-roadside). The occurrence of the target species as well as habitat and vegetation characteristics and the location (GPS) were recorded in each plot as described above.

Data analysis

Altitudinal distribution

All analyses were performed using R (R Development Core Team 2006). We used mixed-effects multiple logistic regression models (Venables and Ripley 2002) to investigate the relationship between altitude and species occurrence and differences in plant responses along the altitudinal gradients between the native and introduced ranges. Models were fitted containing altitude and its second order polynomial, range and their interaction for each species separately, with road nested in range as random effects. Residuals of these models were tested for spatial auto-correlation, which can bias parameter estimates (Dormann 2007). However, spatial autocorrelation of residuals was weak and because models accounting for this correlation structure were qualitatively unchanged from the non-spatial models, only results of the latter are reported. Because many populations of *M. discoidea* at low altitude in the Valais had already senesced when the survey was conducted, all data below 1000 m a.s.l. were excluded from analyses of this species in the Valais. In the Wallowas, *E. annuus* was excluded from all analyses because it was only recorded four times.

The maximum altitude reached by each species in each region was recorded in three ways: 1) the absolute maximum, 2) the mean of the maximum altitudes along each of the seven roads, and 3) the altitude predicted by the logistic regression model at which the probability of finding a species has declined to 10% of its maximum. The latter method underestimates the maximum altitude of a species but has the advantage of minimising the influence of outlier

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populations outside of the "normal" altitudinal range (Becker et al. 2005).

A bootstrapping procedure was used to investigate whether the higher maximum altitude of *L. serriola* in the Wallowas could be explained by its higher overall frequency of occurrence in this region. Occurrences in the Wallowas were resampled (1000 permutations) to decrease the overall frequency to that in the Valais. The predicted maximum altitude in the Valais was then compared to the null distribution of predicted maximum altitudes from the Wallowas assuming equal frequencies of occurrence.

The degree to which species occurrences were aggregated along roads was described using Pearson's correlation coefficient between matrices of resemblance and Euclidean distance between all pairs of plots. Pairs were described as either different (one contains a presence, the other an absence of a given species) or identical (both contain presences or absences; Legendre and Legendre 1998). Separate matrices were constructed for each region, at low and high altitude, for roads in which the species occurred at least five times.

Occurrence in ruderal sites and away from roadsides

Vegetation types in the Valais were classified as "closed" (e.g. forest, shrubland), "open" (e.g. meadow/pasture) and "urban" (e.g. towns/villages, industrial complexes). Forest habitat dominated the roadsides in the Wallowas, but the canopy cover varied greatly: forest with <33% canopy closure above the roadside was classified as "open", and ≥ 33% closure as "closed". Vegetation classes in the Wallowas thus comprised "closed" (closed forest) and "open" vegetation (open forest, grassland habitats and urban areas).

Multiple logistic regression models were fitted to investigate the effects of site characteristics on the occurrence of each species in each region separately. Occurrence was fitted as a function of altitude and its second order polynomial, plot type (verge plot or ruderal site), the dominant vegetation type adjacent to the road, the interaction of transect type with altitude and road as a block effect with no interactions (Newman et al. 1997). The approximate size of the plot (≤ 300 m^2) was included to control for its potential confounding effect on species occurrence. Models for which the dispersion parameter (residual deviance/residual degrees of freedom) was not approximately equal to one were refitted using a quasibinomial link function, which estimates the scale parameter by dividing the Pearson χ^2 by the degrees of freedom (Crawley 2002). The results of the quasibinomial models are reported only when they differed qualitatively from the binomial models. Variable selection was performed by elimination of non-significant terms from the full model based on χ^2 at $p < 0.05$, or with F-tests in the case of quasibinomial models (Crawley 2002).

The degree of invasion of the studied species away from the roadside was assessed by comparing occurrences in plots along transects extending from the roadside into seminatural vegetation. Because species occurrences were very low (range 0–10% across the whole dataset), plots were scored for the presence/absence of at least one of the four North American or four European species. For the same reason, plots were classified simply as roadside/non-roadside without considering the distance of plots from the road. Mixed-effects logistic regression models were fitted with occurrences of native/alien species in each range separately as response variables, dependent on altitude of the roadside plot, plot type (roadside or not) and their interaction, with plot type nested in transect as the random components.

Results

Distribution patterns along altitudinal gradients

All species were more frequent in the introduced range, apart from *Solidago* which tended to be more frequent in the native range (Table 2, Fig. 3). *Conyza canadensis* was only found more frequently in the introduced range

Table 2. Maximum altitudes and frequency of occurrences within their altitudinal range of the study species in both regions. The predicted maximum altitude is the altitude at which the probability of occurrence declines to 10% of its maximum (see text). Also shown are Pearson's correlation coefficients (r) of geograhic distance and the dissimilarity of species occurence between pairs of plots at low and high altitude.

| Species	Range	Freq.	Max. alt.	Mean max. alt.	Predicted max. alt.	r (low)	r (high)
European natives							
Cirsium arvense	Native	0.32	2090	1803	2107	0.01	0.06
	Introduced	0.52	2187	1951	2400	0.12	0.05
Cirsium vulgare	Native	0.09	1826	1516	2252	−0.02	0.08
	Introduced	0.36	2092	1864	2163	0.07	0.09
Cichorium intybus	Native	0.12	1506	991	1185	0.13	0.20
	Introduced	0.13	1753	1450	1394	0.13	0.19
Lactuca serriola	Native	0.27	1401	1153	1292	0.02	−0.02
	Introduced	0.44	1861	1717	1849	0.20	0.07
North American natives							
Conyza canadensis	Native	0.12	1788	1428	1660	0.30	0.21
	Introduced	0.29	1800	1385	1490	0.04	0.09
Erigeron annuus	Native	0.04	1269	1116	NA	NA	NA
	Introduced	0.10	1223	895	909	−0.08	0.09
Matricaria discoidea	Native	0.08	2187	1701	5502	0.09	0.00
	Introduced	0.23	2197	1803	2681	NA	0.03
Solidago	Native	0.14	2160	1899	NA	0.11	0.14
	Introduced	0.07	1530	1096	1456	NA	0.32
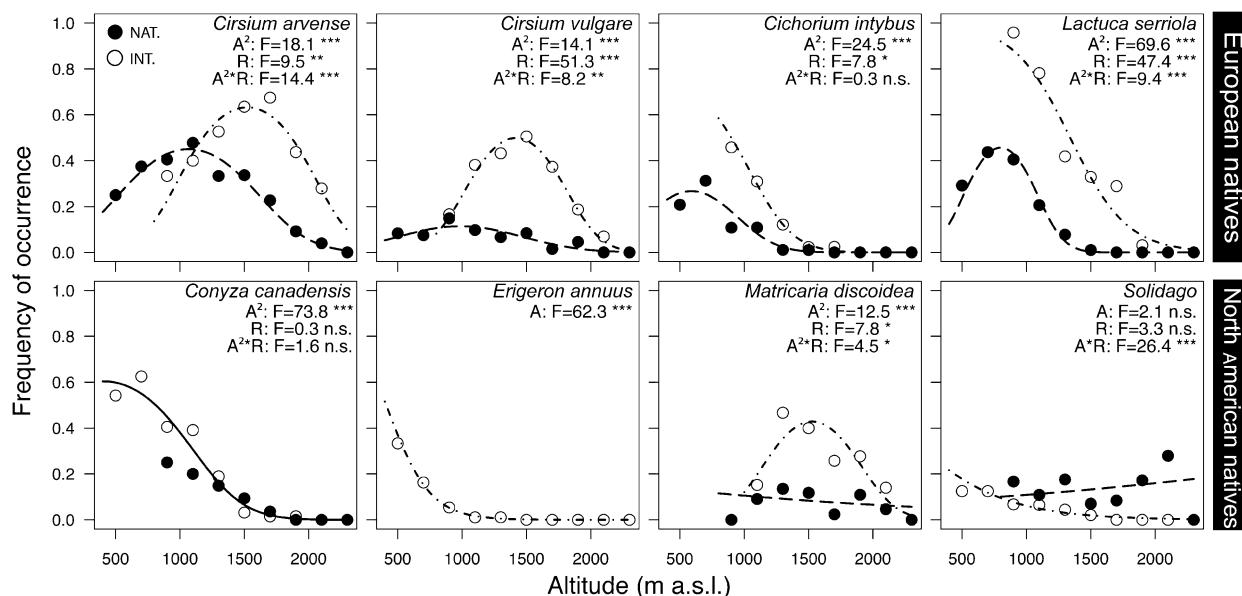
Figure 3. Relationship between altitude and species occurrence in the native ("NAT."; dashed regression lines) and introduced ("INT."; dot-dashed regression lines) ranges. The top four species in the panel are native to Europe and the bottom four native to North America. Denominator degrees of freedom are 12 for the effects of range (R). For the effects of altitude (A) and A × R, degrees of freedom are 884 for *M. discoidea*, 635 for *E. annuus* (introduced range only; see text) and 1062 for all other species. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; "n.s." not significant.

considering altitudes below those found in the Wallowa Mountains. On average, alien plant species were more frequent in the Wallowas (average 32% of plots) than in the Valais (14% of plots). In both the introduced and native ranges, species occurrences usually peaked at intermediate altitudes before declining strongly at higher altitudes (Fig. 3). This pattern was most pronounced for the two *Cirsium* species and for *Matricaria discoidea* in the Valais, which peaked between 1000 and 1500 m a.s.l. In the Valais, *Cichorium intybus*, *C. canadensis* and *Lactuca serriola* peaked in occurrence between 500 and 1000 m a.s.l. For all European natives, the altitude of peak occurrence was shifted upwards in the introduced range by up to 500 m, but there were no consistent differences between ranges for the North American species. For *C. canadensis* and *C. intybus* the rate of change in occurrence with altitude was not significantly different in either range (Fig. 3).

Across all species and in both ranges, the (log) maximum altitude reached by a species was positively related to its (log) frequency within the altitudinal range over which it occurred ($F_{1,12} = 5.1$, $p < 0.05$). Most European species reached higher absolute and mean maximum altitudes across the seven roads in the introduced range (Student's t = 2.89–6.88, DF = 11–12, p < 0.05). However, the mean maximum altitudes reached by *C. arvense* were not significantly different between ranges (Student's t = 1.30, DF = 12, p = 0.22; Table 2), and the predicted maximum altitude of *C. vulgare* was rather higher in the native range. Only *L. serriola* and *C. intybus* reached higher limits in the introduced range, considering all three measures of maximum altitude. The predicted maximum altitude of *L. serriola* in the native range (1290 m a.s.l.; Table 2) was significantly lower than the predictions of the resampled data (one-sided 95% CI = 1730 m a.s.l.) and so cannot be

explained purely by its lower frequency of occurrences in this region. Apart from *Solidago*, which reached a higher maximum in the native range (Student's t = 4.58, DF = 12, p < 0.001), the maximum altitudes of the North American species were not significantly different in either range (Student's t = 0.27–1.34, DF = 7–12, p > 0.22). The predicted maximum altitudes of *C. intybus*, *L. serriola* (native range only), *C. canadensis* and *E. annuus* were substantially lower than the observed maxima, indicating that high-altitude occurrences are outliers to the core distribution of these species.

With the exceptions of *C. intybus*, *C. canadensis* and *Solidago*, there were only weak correlations between species occurrence in plots and the distance between them (Table 2). Occurrences of the European species were generally more aggregated (larger r) at low altitudes in the introduced range, whilst there were only small differences between ranges at high altitudes. Occurrences of *C. canadensis* were substantially more aggregated in the native range, and in the introduced range of *Solidago* (Table 2). Overall there was no tendency for occurrences to be more aggregated at high than at low altitudes.

Species occurrences in ruderal sites and away from roadsides

Alien species were much more frequent in ruderal sites in the Valais than in the Wallowas. In addition, all four North American species were significantly more frequent in ruderal sites in the Valais than in less disturbed verge plots (Fig. 4, Table 3). In contrast, the occurrence of all species native to the Valais (except *L. serriola*) were independent of ruderal sites (Fig. 4, Table 3). In the Wallowas, only *M. discoidea* was more frequent in ruderal sites, whilst *Solidago*
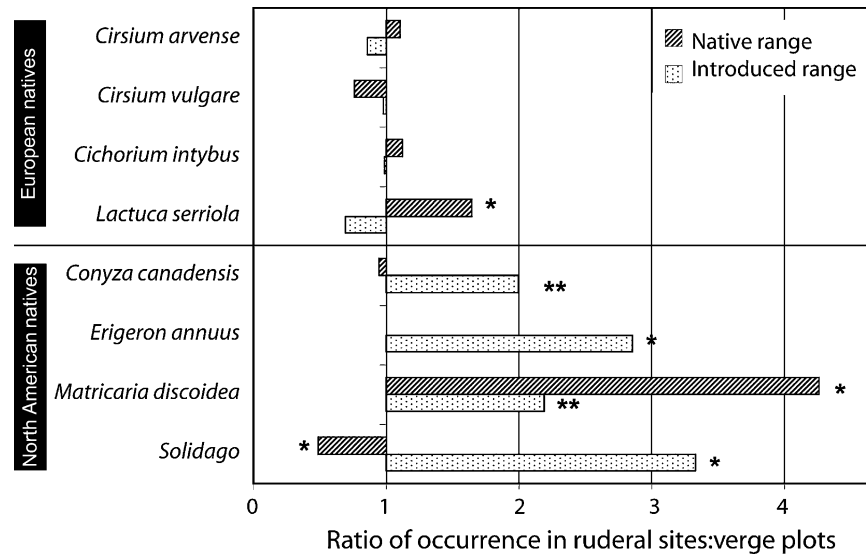
Figure 4. Ratio of species occurrence in ruderal sites and roadside plots. An asterisk indicates a significant relationship between plot type and species occurrence in multiple logistic regression models (* p <0.05, **p <0.001; see text; Table 3).

was significantly more frequent in verge plots. All remaining species were present equally in both types of site. The affinity of most species for ruderal sites did not change along the altitudinal gradients; however, *C. intybus* occurred relatively more often in ruderal sites at higher altitudes while *C. canadensis* occurred less often (significant interactions in the introduced ranges for altitude × plot type; Table 3).

In both regions, alien species tended to occur more frequently in plots adjacent to open/urban vegetation, whilst native species were generally more frequent adjacent to closed vegetation (Table 3). This was true for the introduced *C. canadensis*, *M. discoidea* and *Solidago* in the Valais, and is consistent with their higher occurrence in ruderal sites. Conversely, the European natives *C. arvense*,

C. vulgare and *C. intybus* were significantly more frequent adjacent to closed vegetation. In the Wallowas, the native species *C. canadensis* and *M. discoidea* and the introduced *C. vulgare* were more frequent adjacent to closed vegetation, whilst the alien species *C. intybus* and *L. serriola* were more frequent adjacent to open vegetation.

Both alien and native species were much more common in plots at the roadside than away from it ($F_{1,31} = 11.0-26.5$, p <0.01; Fig. 5). However, aliens in the Wallowas invaded twice as many plots (16%) away from the road than aliens in the Valais (8%). Native species were also more common at the roadside in the Valais than in the Wallowas (Fig. 5). Although altitude had a negative effect on the presence of aliens in both regions (p <0.05), the degree of invasion away from the road did not depend on altitude (p >0.3).

Table 3. Logistic regression models of the effect of altitude (A), plot type (P) and vegetation type (V) on species occurrence after elimination of non-significant terms based on χ^2 at p <0.05. All models contain road as a block factor and plot size as a covariate (not shown). D^2 is the percentage of variation explained by the model.

Species	Range	Model components	Null deviance	Residual deviance	Residual DF	D^2
Cirsium arvense	Native	$-A^2$, V	784	661	626	15.7
	Introduced	$-A^2$	600	514	423	14.4
Cirsium vulgare	Native	$-A$, V	331	307	627	7.2
	Introduced	$-A^2$, V	551	471	422	14.5
Cichorium intybus	Native	$-A$, V	351	230	627	34.5
	Introduced	$-A^2$, P, V, $A^2 \times P$	271	154	419	43.4
Lactuca serriola	Native	$-A^2$, P	551	339	627	38.4
	Introduced	$-A$, V	560	363	423	35.1
Conyza canadensis	Native	$-A$, V*	257	180	423	29.9
	Introduced	$-A^2$, P, V, $A^2 \times P$	696	402	623	42.2
Erigeron annuus	Native	NA	NA	NA	NA	NA
	Introduced	$-A$, P	224	124	628	44.6
Matricaria discoidea	Native	P, V	243	202	423	17.1
	Introduced	$-A^2$, P, V	559	340	448	39.3
Solidago canadensis	Native	P	345	304	424	11.7
	Introduced	$-A$, P, V	236	174	626	26.3

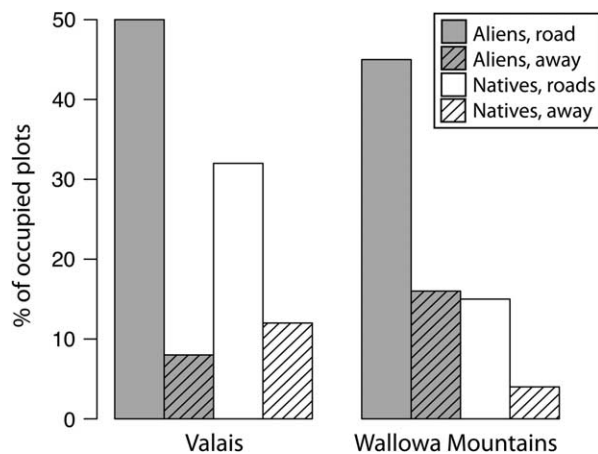*Factor significant in quasibinomial model after correction for under-dispersion (see text).

Figure 5. Percentage of plots occupied by alien/native species within 2 m of the roadside ("road") and in transects extending up to 500 m away from the road into semi-natural vegetation ("away") in each region.

Discussion

Similar responses to altitude between ranges

Plant invasions into temperate mountain systems are likely to be increasingly limited at high altitudes by low propagule pressure and high climatic and biotic resistance (Richardson et al. 2000, Dietz and Edwards 2006). We therefore expected the altitudinal distributions of these eight Asteraceae forbs to be more restricted in their introduced than in their native range. However, the similar maximum altitudes and altitudinal patterns of occurrence between ranges we observed suggest that they are in fact no more limited by factors associated with altitude in the introduced than in the native range. The establishment of these invasion patterns in < 100 yr since introduction indicates that the species are highly plastic in their introduced range (Williams et al. 1995, Parker et al. 2003, Baret et al. 2004) and/or have adapted rapidly along the altitudinal gradients (Lacey 1988, Weber and Schmid 1998, Sexton et al. 2002, Maron et al. 2004). A third possibility, that ecotypes preadapted to different altitudes were independently introduced and "sorted" along the gradients in the new range, seems highly unlikely for all eight species over such small spatial scales. Only *Solidago* showed substantial differences between ranges, which might be attributable to taxonomic differences between the species in the Wallowas and the Valais, or because it was the only species to be more frequent in the native range (see below).

The ecological significance of "altitude" varies from region to region, particularly at different latitudes, and we were therefore careful to select two study areas with climates that were as similar as possible. The fact that most study species reached a similar maximum altitude in both the introduced and native ranges suggests that they are limited by factors that vary similarly with altitude in both regions, such as temperature (e.g. mean annual temperature and heat sum over the growing season) or UV-B (Körner 2007).

Two European species, *C. intybus* and *L. serriola*, reached higher maximum altitudes in the Wallowas, which cannot be explained by differences in their frequency of occurrences

(i.e. a sampling effect) between regions. There may be several, non-mutually exclusive explanations for this pattern. It could result from climatic factors that differ between regions, such as drier conditions at higher altitude in the Wallowas, which might also explain the upward shift in the altitude of peak occurrence of the other European species. Suitable microsites for establishment at high altitude might also be more abundant in the Wallowas, for example due to the greater openness of the roadside vegetation (Poll et al. in press). However, if broad climatic or microsite differences were responsible we would expect some North American species also to have reached higher altitudes in the Wallowas, which was not the case. Another possibility is that *C. intybus* and *L. serriola* have a wider ecological niche in the Wallowas. This could be due to ecological release from enemies in the native range, allowing them to occupy a greater realized niche (cf. DeWalt et al. 2004). Alternatively, the Wallowa populations might stem from native source populations with broader climatic tolerances than Valais populations, or have evolved a broader tolerance in the Wallowas due to higher genetic variation within and across populations (Ellstrand and Schierenbeck 2000). In support of this hypothesis, populations of *L. serriola* in the Wallowas were found to have significantly greater diversity at seven microsatellite loci than Valais populations (Alexander 2007).

Low propagule pressure (i.e. dispersal limitation) has also not prevented these species from reaching high altitudes in the new range. Indeed, the higher maximum altitudes of the European species in the Wallowas might be partly driven by a higher propagule pressure in this region, where the plants are on average nearly twice as frequent than in the Valais (Levin 2006, Wilson et al. 2007). Some evidence for dispersal limitation (or a lack of "safe sites" for establishment) might be found in the more aggregated occurrences of the European species at low altitude in the Wallowas (Dormann 2007). However, overall these limitations appear to be no more prevalent in the introduced than in the native range. That most species reached their limits within the altitudinal range of most of the roads also suggests that these are more influenced by climate than by propagule pressure. It could be that propagule pressure is most important in the early stages of an invasion when a population is not yet in equilibrium with its environment.

Region-specificity of invasion patterns

Differences in introduction history might partly explain why the occurrence of alien species in the Wallowas was more than twice that in the Valais. For example, intensive introductions of Eurasian species to North America, particularly associated with agriculture, has often led to high levels of genetic variation (e.g. Neuffer and Hurka 1999, Novak and Mack 2005), and their spread has been nurtured by management practices such as mowing and cattle-grazing to which they are pre-adapted (di Castri 1989, Mack and Erneberg 2002). Many North American species have also been introduced deliberately to Europe, but mainly as ornamentals (*Solidago* spp.; Weber and Schmid 1998, *E. annuus*; Hegi 1979) and without intensive propagation and dispersal.

The clear regional differences in the importance of ruderal sites for alien plants may reflect contrasts in land use and disturbance regimes. Aliens in the Valais may be excluded from roadside verges by competition with native species that are better adapted to local management practices, in particular mowing (Baker 1974). In the Wallowas, management by grading of the roads, logging and cattle-grazing activities cause more soil disruption and vegetation openness, so that establishment of both native and alien ruderal species is promoted along the length of roads and not just in ruderal sites. This might also partly explain why the Wallowas are more highly invaded than the Valais, both at and away from the roadside. Consistent with this suggestion, seedling establishment of these species was positively related to disturbance in the Valais, but not in the Wallowas where all experimental plots were open and rather disturbed (Poll et al. in press, but see Paiaro et al. 2007).

At least some of the observed differences between the Valais and Wallowas might be due to traits of the species themselves. For example, the North American species have smaller seeds than the European species (Alexander et al. in press). Seed size affects the success of seedling establishment (Moles and Westoby 2004), and so the North American species might be more limited by disturbance (Burke and Grime 1996, Poll et al. in press).

Implications for plant invasion along altitudinal gradients

The strong similarity in altitudinal distribution patterns in both native and introduced areas resemble parallel clines in quantitative traits of these species observed by Alexander et al. (in press) along the same altitudinal gradients. Genetically based clines have been shown for other alien species in response to gradients of latitude (Huey et al. 2000, Maron et al. 2004, 2007) and continentality (Leger and Rice 2007). These observations suggest that species niches are usually conserved between ranges (Wiens and Graham 2005, Holt et al. 2005), despite the profound ecological (e.g. biotic interactions, selection pressures) and genetic (e.g. admixture, gene flow) changes that can accompany the introduction of a species to an area isolated from the ancestral range (Lee 2002, Levin 2003, Holt et al. 2005).

Our data suggest that whilst niche boundaries provide the fundamental constraints to invasion (e.g. the altitudinal limit), changing climatic conditions along environmental gradients within the niche (i.e. the altitudinal range) are likely to pose only transitory and limited constraints to the spread of alien plants into high mountain areas. This is either because invading populations are highly plastic and/ or are able to adapt rapidly to local environmental conditions. This implies that the decrease in numbers of alien species with altitude observed in most temperate mountain systems is explained by an absence of mountain plants from the alien flora, rather than a reduced ability of invaders to adapt to changing climatic conditions (Becker et al. 2005, McDougall et al. 2005).

In general we found the annual species to have more restricted altitudinal distributions, with the highest occurrences consisting only of scattered individuals (cf. Körner

2003). We would therefore expect perennial species, and especially clonal plants such as *C. arvense* and *Solidago*, to be more successful invaders of high altitudes. However, the success of annual species such as *M. discoidea* might be explained by characteristics such as a rapid life-cycle and low stature that enable them to escape the seasonally adverse climatic conditions at high altitudes (Körner 2007).

The relative importance of ruderal sites as refugia from biotic constraints and sites of high propagule/nutrient availability generally did not change along the altitudinal gradients (cf. Petryna et al. 2002). However, our data suggest that, within a species-specific altitudinal range and given sufficient plasticity/genetic variation in invading populations, plant invasions along environmental gradients are likely to be more constrained by changing patterns of disturbance and biotic interactions (e.g. competition with native vegetation) than by climatic factors (Poll et al. in press). This is likely to be especially the case for invasions advancing into less disturbed semi-natural vegetation (Dietz and Edwards 2006). Experiments manipulating competition and climatic factors are now needed to test this prediction. However, the greater ecological amplitude of *L. serriola* and *C. intybus* in the introduced range raises the intriguing possibility that novel evolution may sometimes enable introduced populations to invade environments outside the niche constraints existing in the native range (Ellstrand and Schierenbeck 2000, Broennimann et al. 2007).

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